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Plant communities of high-Andean *bofedal* wetlands across a trans-Andean transect in southern Peru

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Abstract

Aims: Ecosystems of the Tropical Andes include plant communities above 4,000 m in elevation, associated with wetlands known as *bofedales*. To enhance our understanding of them, we surveyed *bofedal* plant communities in the Peruvian Andes. **Questions:** Which are the most common *bofedal* plant communities, and what are their main characteristics? **Study area:** An east-to-west 68 km megatransect in Ayacucho and Huancavelica departments in Peru, the area of influence of a gas pipeline. **Methods:** We surveyed 127 (1 m × 1 m) permanent plots annually between 2017 and 2019 to assess plant communities, calculated diversity metrics, and applied non-parametric hypothesis testing analysis of similarities and multivariate analyses to the data. **Results:** We identified 13 plant communities with 3.5 to 11.7 mean species richness. Only seven were statistically different; the other six were rare and require additional surveys to define their status as independent communities. The *Distichia muscoides*-dominated community was found in most sites (90%), plots (55%), and along the entire elevational range we studied. *D. muscoides*, *Plantago tubulosa*, and *Rockhausenia pygmaea* were the most frequent species in the studied *bofedales* (in 30 of 31 sites). These species are usually cushion or carpet forming, so average plant cover was high in most plant communities where they occurred (89–98%). The seven plant communities (dominated by *D. muscoides*, *R. pygmaea*, *Plantago tubulosa*, *P. rigida*, *Lachemilla diplophylla*, *Aciachne pulvinata* and *Juncus stipulatus*) were consistent in their structural and compositional characteristics and maintained differences between them during our three-year study. **Conclusions:** We show that *bofedal* plant communities in the southern Peruvian Andes are more heterogeneous than the four broad types previously reported. This heterogeneity occurs at local site levels but also at landscape and regional scales. We highlight the importance of considering this heterogeneity when discussing and implementing management, restoration, and conservation actions in *bofedales*.

Taxonomic reference: WFO (2024)

Keywords

Alpine vegetation, Andes, *bofedal*, diversity, peatland, Peru, wetland

PENSOFT

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Introduction

The tropical Andes, a global biodiversity hotspot, contain diverse ecosystems and habitats (Young et al. 2007). A major factor contributing to this diversity is the east–west humidity gradient in the Central Andes, reflected in the differentiation of the humid Puna towards the eastern flanks and the dry Puna (Josse et al. 2009) facing the Pacific slopes (Killeen et al. 2007; Espinoza et al. 2015).

Within this gradient, the Central Andes contain plant communities above 4,000 m a.s.l. which are associated with wetlands and water-saturated soils. These communities are known by several local names ("turbera" in Colombia and Ecuador; *bofedal* in Ecuador, Peru and Bolivia, "vegas" or "mallines" in Chile and Argentina, Hergoualc'h et al. 2022). These wetlands are patchy and island-like in nature and are usually surrounded by large swards of grasslands and drylands. At the local level, they have a consistent and characteristic set of plant species, but at regional levels, plant abundances and composition are influenced by environmental factors such as elevation, topography, hydrology, geology, and wildlife grazing (Ruthsatz 2012; Valencia et al. 2013; Salvador et al. 2014; Oropeza 2019; Portal-Quicaña 2019; Izquierdo et al. 2020; Domic et al. 2021; Monge-Salazar et al. 2022). In addition to these natural factors, human uses of the *bofedales* (e.g., grazing areas for native and introduced livestock, water use, peat extraction) have also been deemed important in influencing their ecological processes and plant community composition (Ruthsatz 2012; Maldonado-Fonkén 2014; Chimner et al. 2019; Yager et al. 2019; Navarro et al. 2023).

According to the National Institute for Research on Glaciers and Mountain Ecosystems (INAIGEM), the *bofedales* in Peru include four major types of plant formations, named after the life-form(s) of the dominant and most conspicuous species: cushions (formed by e.g. *Distichia muscoides*, *Oxychloe andina*, *Plantago rigida*), carpets (e.g. *Plantago tubulosa*, *Rockhausenia pygmaea*), grasses and graminoids (e.g. *Festuca* spp., *Calamagrostis* spp., *Carex* spp., *Eleocharis* spp., *Phylloscirpus* spp.), and mosses and shrub wetlands (formed by e.g. *Sphagnum* spp., *Andicolea* spp.). *Bofedales* dominated by cushions are the most frequent type, especially in central and southern Peru. INAIGEM highlighted the heterogeneity of these ecosystems at vegetation and hydrological levels. Still, little information is available on grass- and graminoid-dominated and carpet *bofedales*, as well as on *bofedales* subjected to strong seasonal water availability (saturated only in the rainy season; INAIGEM 2023).

The INAIGEM classification, the first of its kind at national level, is based on previously published information for *bofedales* vegetation in Peru (Cooper et al. 2010; Ruthsatz 2012; Maldonado-Fonkén 2014; Salvador et al. 2014; Maldonado-Fonkén 2018; Polk et al. 2019; Portal-Quicaña 2019), expert consultations and ongoing studies. Similar plant formations have been described for Colombia, Ecuador, Bolivia, and Argentina (Ruthsatz 2012; Benavides and Vitt 2014; Loza Herrera et al. 2015; Ruthsatz et al. 2020; Domic et al. 2021; Izquierdo et al. 2022; Suarez et al. 2022). Several plant communities or even mixed communities within a single site have also been reported (Ruthsatz 2012; Maldonado-Fonkén 2014). Nevertheless, most of these studies focused on the dominant species and physiognomy of the plant communities, so a more comprehensive description is needed.

Within the framework of the Biodiversity Monitoring and Assessment Program (BMAP), a collaboration between the Smithsonian Institution and the PERU LNG company set in the southern Andes of Peru (Dallmeier et al. 2013), we studied the vegetation of the high-Andean wetlands along an east to west 68 km-long megatransect from Ayacucho to Huancavelica departments.

This contribution aims to identify and characterize the most common *bofedal* plant communities along the megatransect. In doing so, we attempt to answer the following guiding questions: Is *Distichia muscoides* the only dominant species, as commonly treated? How do patterns of diversity, structure, and composition of plant communities change along the megatransect? Are the diversity and vegetation cover values high or low compared with other reports? Can selected environmental factors, such as soil moisture and water table depth, explain floristic and plant community patterns?

Study area

Our study area corresponds to the area of influence of the PERU LNG pipeline (LNG: liquified natural gas, Figure 1, Table 1), encompassing a variety of habitats between 4,200 and 4,900 m a.s.l. along 68 km from the southwest to the northeast of the Central Andes, in the departments of Ayacucho and Huancavelica in Peru. Precipitation follows a seasonal pattern, with 60–90% of total rainfall between December and March (Langstroth et al. 2013). For the evaluation sites the total annual precipitation values according to PISCO (Peruvian Interpolated data of SENAMHI's Climatological and hydrological Observations), range from 480 mm to 817 mm, with site KP 164 + 500 reaching 1232 mm (Aybar et al. 2019). Average monthly precipitation in the dry season (June–August) ranges from 3.3 to 12.2 mm, and in the wet season (January–March) from 107 to 130 mm (Aybar et al. 2019). Mean air temperatures range from 9.7 °C to 19.7 °C, with minimum temperatures reaching values below 0 °C at night (Valencia et al. 2013). The study area overlaps with several rural Andean communities, where traditional husbandry of alpacas, lamas, and sheep (introduced) is common.

Methods

We surveyed plant communities of 31 *bofedales* along our study transect, located between 4,265 and 4,855 m a.s.l. According to previous studies using satellite images (PERU LNG, not published), *bofedales* were reported to have sizes between 1.25 and 43.98 ha, although we observed sites smaller than 1 ha in the field. We did the assessments annually during the austral dry season (June–July) from 2017 to 2019. In 2017, we set up randomly

Table 1. *Bofedal* study sites in the southern Peruvian Andes.

No.	Site ID	UTM Coordinates (WGS84, 18L)		Elevation (m a.s.l.)	Number of plots	Monitoring wells
		E	N			
1	132+850	-74.50292135	-13.28192729	4,301–4,304	4	-
2	138+000	-74.54629416	-13.28596879	4,573–4,575	5	1
3	140+880	-74.57035634	-13.29443795	4,566–4,581	3	1
4	145+340	-74.60595285	-13.30802288	4,665–4,668	3	-
5	147+308	-74.62303259	-13.30278615	4,687–4,699	4	1
6	149+270	-74.63785065	-13.29687591	4,707–4,716	6	
7	150+800	-74.64953935	-13.29020998	4,489–4,507	4	-
8	152+800	-74.66311571	-13.27994714	4,528–4,537	6	-
9	153+000	-74.66438133	-13.27932488	4,537–4,561	2	1
10	153+170	-74.6658498	-13.27888374	4,594–4,605	2	-
11	154+099	-74.67328382	-13.27710299	4,660–4,666	3	-
12	154+372	-74.67505366	-13.27911266	4,647–4,648	3	-
13	154+700	-74.67834744	-13.28062693	4,672–4,673	4	-
14	158+470	-74.70899211	-13.29287104	4,818–4,826	7	-
15	162+365	-74.74256575	-13.29731089	4,848–4,850	3	1
16	163+760	-74.75422408	-13.29975484	4,798–4,802	3	-
17	164+250	-74.75856181	-13.30140472	4,745–4,758	4	-
18	164+700	-74.76191007	-13.30472645	4,727–4,735	4	1
19	165+500	-74.7673449	-13.3082309	4,801–4,810	3	-
20	167+640	-74.78545257	-13.30631175	4,825–4,829	4	-
21	168+250	-74.78972555	-13.30850359	4,777–4,778	4	-
22	168+500	-74.7918393	-13.30922873	4,745–4,752	3	-
23	168+750	-74.79468335	-13.30891456	4,715–4,718	3	-
24	170+100	-74.80589219	-13.309059	4,686–4,687	5	-
25	171+100	-74.81293477	-13.31202117	4,721–4,726	4	-
26	195+500*	-74.98609111	-13.37539601	4,531–4,547	5	1
27	198+000	-74.98406711	-13.39648287	4,596–4,605	5	2
28	4SI	-74.52708698	-13.28360093	4,265–4,299	6	-
29	6SIad	-74.76143284	-13.30177817	4,722–4,728	4	1
30	6SI	-74.75980718	-13.3024729	4,733–4,736	5	2
31	NC12	-74.79573822	-13.30617555	4,661–4,666	6	1

*: this was the only site with a rock fence.

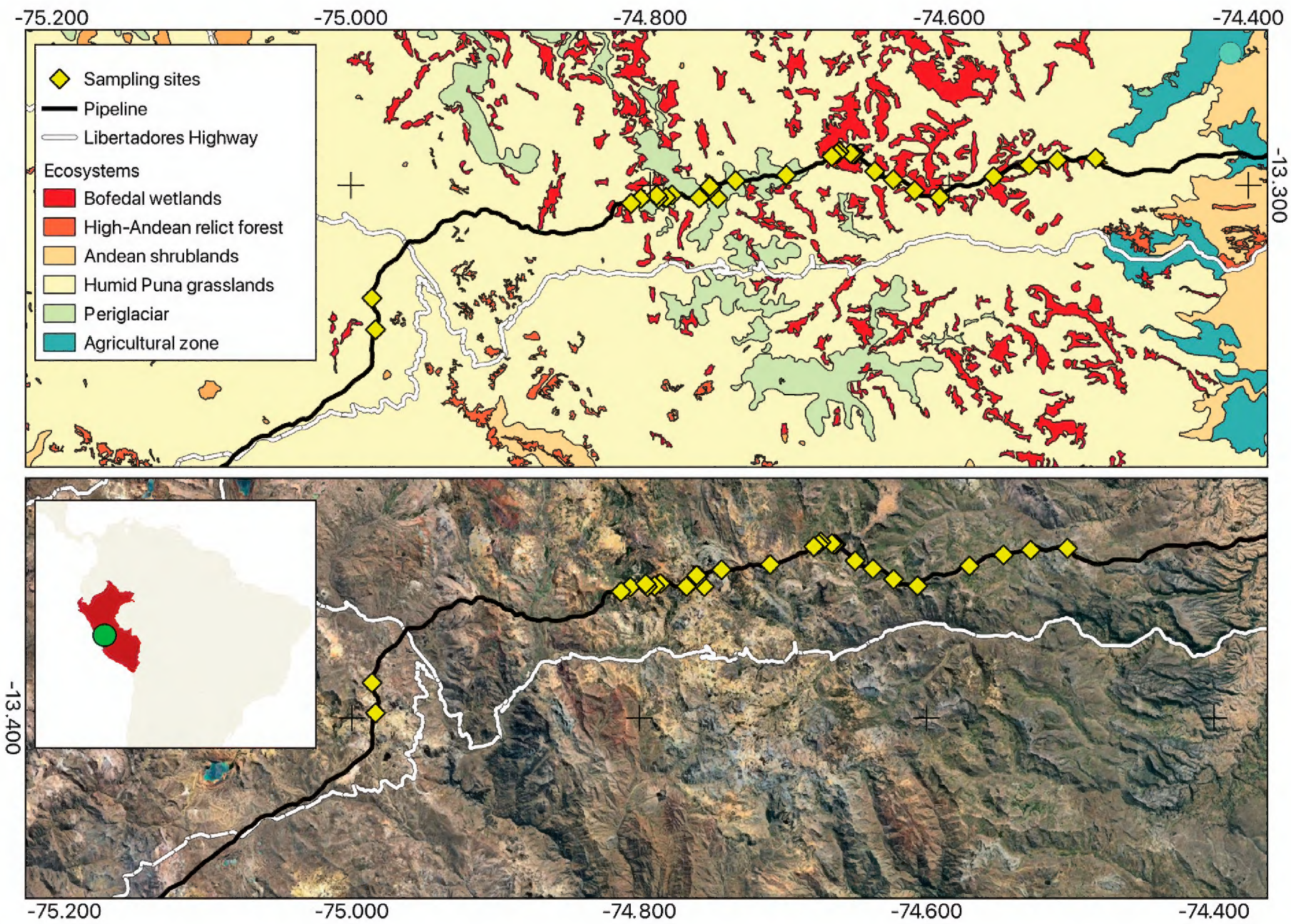

Figure 1. Location of *bofedales* and main ecosystems in the study area. The map inset shows the position of Peru within South America and the approximate study area, indicated by a green dot. The ecosystems shapefiles used are from Peru's Ecosystem Map (MINAM 2019).

distributed 1 m × 1 m permanent plots in homogeneous patches of the dominant vegetation to characterize the plant communities in each *bofedal*. Per *bofedal*, we surveyed between two and seven plots (Table 1). The number was established considering the surface area of the *bofedal*, its heterogeneity (different plant communities), and the resources available for research. 378 plots were surveyed in the three years, 127 in 2017 and 2019, and 124 in 2018 (the missing plots could not be relocated).

We surveyed plant cover (per species) and ground cover with the point intercept method using a grid quadrat frame (Bonham 2013), considering 100 points (crossing points of the thread from the quadrat) per plot. The percentage cover for each species will equal the number of points in which the species was recorded. In subsequent years, we returned to each plot using coordinates and photographs (Suppl. material 1) and recorded the same plot area during each survey (Suppl. material 2; Linares-Palomino and Maldonado-Fonkén 2023).

We recorded cover estimates of several strata (ground cover) as useful proxies of degradation and potential habitat preferences of plant communities and species. We used the following categories: vegetation (vascular plants), moss, bare soil (or peat), dead vegetation, wildlife and livestock dung, rock, and water.

We used information on soil moisture and water table depth from the BMAP. We measured soil moisture (only in 2017) in 71 plots (2–3 records per plot) of ten plant communities (Table 2), with a ML3 ThetaProbe Soil Moisture Sensor from Delta-T Devices (UK), configured for organic soils. The water table monitoring wells were located at 11 sites (Table 1) and in six plant communities (Table 2). Using a peat sampler from Royal Ejelkamp (The Netherlands) we made a 50.8 mm diameter hole, where we inserted a PVC tube of the same size. Water table measurements were taken between July 2017 and December 2019, every one or two months in the first two years, and only in January and December of the last year. The number of sites, plots, soil moisture measurements, and monitoring wells per plant community are presented in Table 2.

We collated a list of species and morphospecies based on field collections and surveys done by the BMAP since 2009 (Valencia et al. 2013). We followed APG IV (The Angiosperm Phylogeny Group et al. 2016), and scientific names and authorship followed The World Flora Online (WFO 2024). Species were primarily identified in the field by a team of experienced *bofedal* botanists and ecologists (MM, HC). However, when plant material was fragmentary and/or lacked fertile structures, we collected and photographed samples and checked them against specialized literature (Tovar 1993; Gonzáles 2015; Sylvester et al. 2016) or referred them to specialists. We used the morphospecies concept on collections that were difficult to identify at the species level but otherwise had morphological characters that unequivocally differed from all the other material already identified in the area.

Since *bofedal* communities are associated with water-logged conditions, some species thrive in moist or saturated soils (hydrophytes and others). These were defined as moisture indicators (Suppl. material 3) based on our field observations and literature (Kahn et al. 1993; Tovar 1993; Gonzáles 2015; Meneses et al. 2015).

Data analyses

To determine whether plant communities differed in composition and abundance (cover), we performed a one-way Analysis of Similarities (ANOSIM) on a plot × species matrix using the Bray-Curtis index (Bray and Curtis 1957) with PAST 4.12b (Hammer et al. 2001). We identified the species with the highest cover and the most frequent companion species for each plant community. To further describe each community, we calculated their species richness, Pielou's evenness (Pielou 1966) and estimated the percentage of each ground cover type per community.

We used a non-parametric Analysis of Variance with the Kruskal-Wallis test (Kruskal and Wallis 1952) with InfoStat version 2019 (Di Rienzo et al. 2019), to identify significant statistical differences ($p < 0.050$) in richness, evenness, vegetation cover, cover of moisture indicators, soil moisture and water table depth between plant communities.

We applied a Hellinger transformation on the raw plant cover values of a plot × species matrix across years (2017–2019) to visualize the variability in species composition and abundance through non-metric multidimensional

Table 2. Number of sampling units per plant community: vegetation, soil moisture, and monitoring wells. 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2. Soil moisture measurements were done with the vegetation assessment in 2017. Water table measurements (monitoring wells) were taken in five months of 2017 (July, September, October, November, and December), four in 2018 (February, May, July, and September), and two in 2019 (January and December).

Number of		Plant communities													Total
		1	2	3	4	5	6	7	8	9	10	11	12	13	
Sites		28	13	8	7	5	1	1	1	1	1	1	1	1	**31**
Vegetation plots per year	2017	69	23	10	9	6	2	2	1	1	1	1	1	1	**127**
	2018	69	22	10	9	5	2	1	1	1	1	1	1	1	**124**
	2019	69	23	10	9	6	2	2	1	1	1	1	1	1	**127**
Soil moisture (2017)	n	121	38	18	6	6	6	6	-	3	3	-	3	-	**210**
	plots	41	13	6	2	2	2	2	-	1	1	-	1	-	**71**
Monitoring wells (2017–2019)	n	5	4	2	-	-	1	-	-	-	-	-	-	1	**13**
	N° sites	4	3	2		-	1	-	-	-	-	-	-	1	**11**

scaling (NMDS) using a dissimilarity matrix of Bray-Curtis distances (Legendre and Gallagher 2001). We complemented the characterization of the plant communities by calculating and plotting sample-based rarefaction curves based on Hill numbers (q = 0, species richness) using incidence data (frequency) from the complete species pool of each surveyed plot (combined data from 2017–2019). We then used a Principal Component Analysis (PCA) to explore how the identified communities were distributed according to five community descriptors: plant cover, bare soil, species richness, Pielou's evenness, and cover of moisture indicators. To perform the PCA, we calculated the mean value of those descriptors for each plant community in a given year. We used the "vegan" package (Oksanen et al. 2022) for both the NMDS and PCA analyses, and the "iNEXT" package for rarefaction curves (Hsieh et al. 2016).

Results

Bofedal plant communities in southern Andean Peru

Based on the species' dominance (i.e. plant cover) and compositional patterns, we identified 13 plant communities (Figure 2) with mean species richness between 3.5 to 11.7 (Table 3). In most cases, they have one clearly dominant species (mean cover 40–70%, Figure 3), but two were mixed communities in which at least two species shared dominance (each species with cover values of 10–22%). Seven of these communities (Group 1) differed statistically (ANOSIM, Bray-Curtis, $p < 0.050$, Table 4, Suppl. material 4). The other six communities (Group 2) were rare (one plot per year each) and did not have statistical

Table 3. General characteristics of *bofedal* plant communities in the southern Peruvian Andes. ⁺: Mean; *Other ground cover categories reached more than 10% in two communities. *Aciachne pulvinata* (dead vegetation: 11.33±4.03) and Mixed community 2 (bare soil 33±12.7%). **Total richness is correlated with sampling effort (Table 2). Water table measurements are negative. 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

		Plant communities												
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Environmental variables														
Elevation (m)		4,292–4,850	4,299–4,798	4,374–4,726	4,265–4,801	4,284–4,718	4,722–4,733	4,531–4,533	4277	4749	4826	4301	4825	4850
Soil moisture (%)⁺		79.1±1.9	62.6±2.6	55.3±4.8	100	68.6±12.9	63.9±6.1	76±7.9	-	45.1±15.2	100	-	19.7±0.9	-
Water table (cm)	Mean	8.6±3.3	30.9±5.1	43.4±9.9	-	-	47.6±12.8	-	-	-	-	-		19±10.4
	Max	87	95	200	-	-	140	-	-	-	-	-		94
Other characteristics														
Vegetation cover (%)⁺		95.2±0.5	93.7±0.6	92.2±1.6	91.7±1.4	93.6±1.2	74.8±8.1*	91.4±4.7	98±1	89±1	95.3±2.2	89.7±3.3	89.3±0.9	66.3±12.1*
Cover of moisture indicators (%)⁺		94.1±0.6	92.3±0.7	91.2±1.9	89±1.7	92.8±1.3	72.8±8.9	91.4±4.7	97.3±0.3	89±1	95.3±2.2	88.7±3.7	71.7±7.7	64.7±10.7
Richness per plot	Total**	55	38	20	32	26	18	10	9	9	11	15	18	13
	Range	1–12	5–15	1–7	5–13	3–12	3–13	6–8	5–6	3–9	5–9	10–11	11–13	6–10
	Mean	6.5±0.2	8.2±0.3	3.6±0.3	8.4±0.4	7.4±0.6	8±1.8	6.8±0.4	5.7±0.3	5.7±1.8	7.3±1.2	10.7±	11.7±0.7	8±1.2
Pielou index		0.53	0.70	0.38	0.69	0.61	0.58	0.75	0.54	0.63	0.76	0.78	0.86	0.71

Table 4. Cover of dominant species (dark grey background) including those with more than 15% in at least one plant community. Plant communities with different superscripts differ significantly (ANOSIM Bray Curtis, $p < 0.05$). Values are mean percentage cover from annual survey data (2017–2019). Plant community names correspond to those of the dominant species: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

	Plant community (cover per species in %)												
	1[a]	**2[b]**	**3[c]**	**4[d]**	**5[e]**	**6[f]**	**7[gi]**	**8[h]**	**9[h]**	**10[h]**	**11[h]**	**12[h]**	**13[hi]**
Dominant species in one or more community													
Aciachne pulvinata	7.0	2.0	3.5	2.1	1.0	44.2	-	-	-	-	-	4.0	2.0
Calamagrostis chrysantha	3.5	-	-	-	-	-	-	-	54.0	-	-	-	-
Calamagrostis rigescens	4.4	4.3	-	6.6	7.0	2.0	17.6	70.3	12.0	-	2.3	1.0	-
Calamagrostis vicunarum	3.2	2.1	7.5	5.1	1.5	3.0	-	-	-	-	-	22.5	-
Distichia filamentosa	-	-	-	-	-	-	-	-	-	40.3	-	-	-
Distichia muscoides	66.2	10.3	1.8	7.8	5.8	4.7	-	-	12.0	-	1.0	9.3	17.0
Eleocharis albibracteata	3.0	8.3	1.0	8.6	8.2	14.0	-	5.0	-	-	15.0	1.0	21.3
Juncus stipulatus	1.6	1.3	-	-	3.7	3.5	40.4	7.0	-	-	4.0	-	-
Lachemilla diplophylla	10.4	5.7	-	13.0	54.4	1.3	11.2	-	7.7	-	3.0	10.3	5.3
Lobelia oligophylla	6.2	3.0	1.0	6.9	7.1	5.0	1.5	1.5	-	-	40.3	-	1.0
Plantago rigida	4.9	4.6	79.4	6.7	-	-	-	-	-	-	-	-	-
Plantago tubulosa	7.0	16.4	2.5	46.3	10.6	3.0	1.7	11.0	5.0	4.0	4.0	10.3	9.0
Rockhausenia pygmaea	3.5	43.6	1.0	8.3	11.2	13.3	2.5	1.0	1.0	6.0	2.0	7.3	2.0
Other species													
Phylloscirpus cf. *acaulis*	3.6	10.2	-	4.0	3.6	1.3	-	-	-	24.0	1.0	-	5.5
Zameioscirpus muticus	9.8	2.0	-	-	-	-	-	-	-	21.7	-	-	-

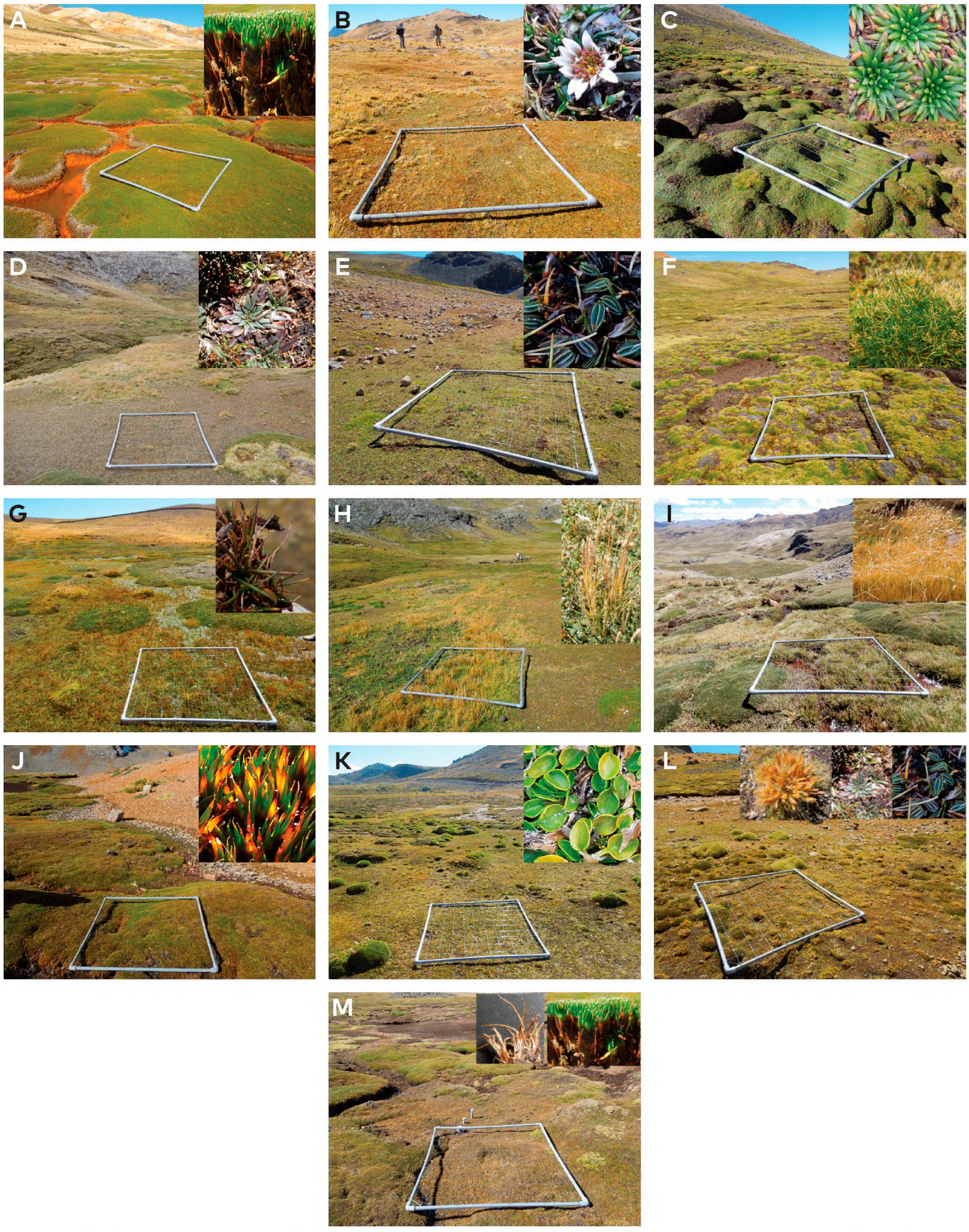

Figure 2. *Bofedal* plant communities in the southern Peruvian Andes. Plant communities: A: *Distichia muscoides*, B: *Rockhausenia pygmaea*, C: *Plantago rigida*, D: *Plantago tubulosa*, E: *Lachemilla diplophylla*, F: *Aciachne pulvinata*, G: *Juncus stipulatus*, H: *Calamagrostis rigescens*, I: *Calamagrostis chrysantha*, J: *Distichia filamentosa*, K: *Lobelia oligophylla*, L: Mixed community 1 (*Calamagrostis vicunarum*, *Plantago tubulosa*, *Lachemilla diplophylla*), M: Mixed community 2 (*Eleocharis albibracteata*, *Distichia muscoides*). The pictures also include the quadrat frame used for the point intercept grid-quadrat method.

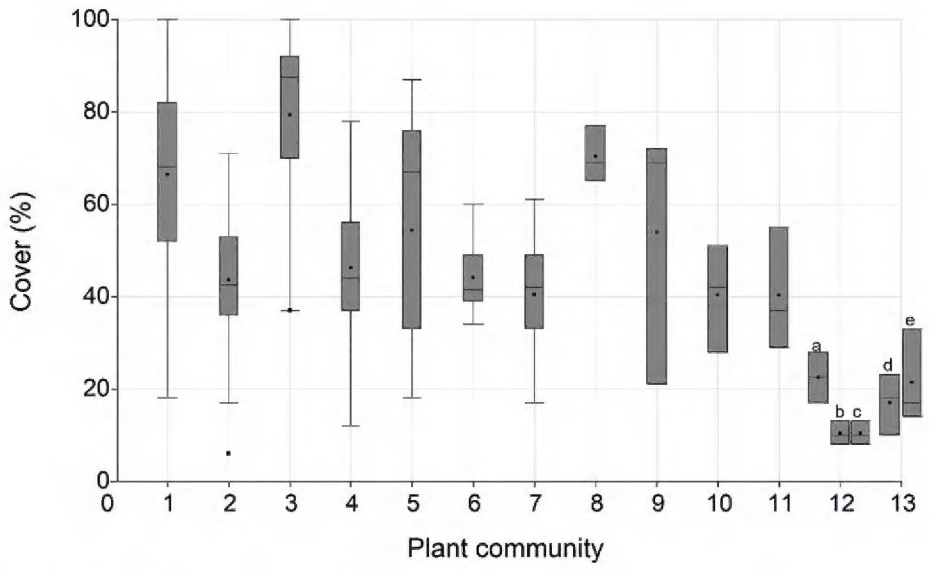

Figure 3. Box plots of the cover of dominant species per plant community. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1 (a: *Calamagrostis vicunarum*, b: *Lachemilla diplophylla*, c: *Plantago tubulosa*), 13: Mixed community 2 (d: *Distichia muscoides*, e: *Eleocharis albibracteata*).

support (ANOSIM, Bray Curtis $p > 0.050$), sharing similarities with at least five other communities.

Environmental variables (elevation, soil moisture, water table depth) and other characteristics (vegetation cover, cover of moisture indicators, species richness, Pielou index) per community are presented in Table 3 and Figure 4. The cover of dominant species, including those with more than 15% cover in at least one plant community, is presented in Table 4. Frequent companion species are presented in Table 5. Detailed information per plant community, including all the species and their frequencies, is available in Suppl. material 3.

Communities are presented from the most to the least common, according to their frequency in the study area. Plant communities were named after dominant species. The ones outlined below, correspond to the seven well defined communities (Group 1):

1. *Distichia muscoides* community: A cushion-type community usually with pools, high soil moisture values, and a shallow mean water table depth. It was widely distributed in the study area, occurring in the

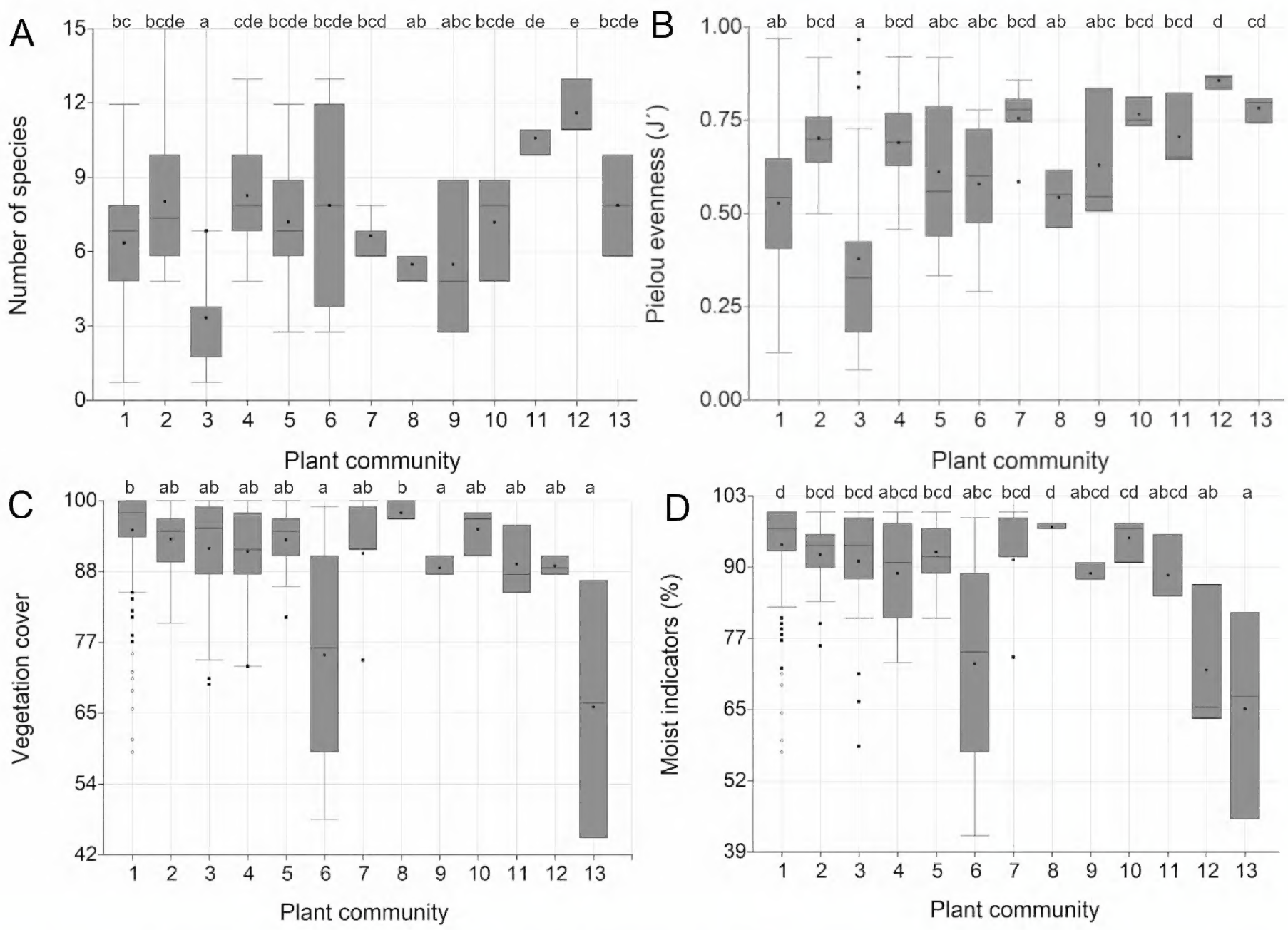

Figure 4. Box plots of A) number of species, B) Pielou's evenness, C) vegetation, and D) moisture indicators cover per square meter in each plant community. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2. Communities with a common letter are not significantly different (Kruskal Wallis Test, $p > 0.050$). Inside each box, horizontal line and dot represent the median and mean values, respectively.

Table 5. Species with highest frequency (%) per plant community. Includes dominant species (dark grey background) and frequent companions (in bold). Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

Species	Plant community (frequency per species in %)												
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Aciachne pulvinata	9	22	40	30	12	100	-	-	-	-	-	33	33
Calamagrostis chrysantha	2	-	-	-	-	-	-	-	100	-	-	-	-
Calamagrostis rigescens	22	21	-	30	59	17	**100**	100	67	-	**100**	33	-
Calamagrostis spicigera	30	50	**50**	37	-	-	-	-	-	67	-	67	-
Calamagrostis vicunarum	9	16	13	26	12	50	-	-	-	-	-	67	-
Carex sp.	18	22	10	41	6	33	-	67	-	67	-	**100**	-
Cotula mexicana	5	4	-	19	47	-	**100**	67	33	-	100	-	-
Distichia muscoides	100	56	17	44	29	50	-	-	**100**	-	67	**100**	100
Distichia filamentosa	-	-	-	-	-	-	-	-	-	100	-	-	-
Eleocharis albibracteata	15	**90**	3	**63**	**65**	33	-	67	-	-	**100**	67	100
Hypochaeris taraxacoides	21	53	33	**67**	24	-	-	-	-	-	**100**	-	33
Juncus stipulatus	5	4	-	-	18	33	100	33	-	-	-	-	33
Lachemilla diplophylla	48	66	-	48	100	50	**100**	-	**100**		67	100	**100**
Lilaeopsis macloviana	4	4	-	11	29	33	**100**	-	-	-	-	-	-
Lobelia oligophylla	31	31	7	52	47	**100**	40	67	-	-	100	-	33
Plantago tubulosa	**63**	**97**	13	100	**88**	50	60	**100**	33	33	**100**	100	**100**
Plantago rigida	4	7	100	11.11	-	-	-	-	-	-	-	-	-
Rockhausenia pygmaea	**57**	100	7	**85**	53	50	40	33	33	**100**	67	100	67
Rockhausenia solivifolia	12	6	-	-	-	-	-	-	-	**100**	-	-	-
Zameioscirpus muticus	30	1	-	-	-	-	-	-	-	**100**	-	-	-

largest number of sites, plots, and elevational ranges. Its mean richness per square meter (7) was significantly higher than that of the *Plantago rigida* community (4) but lower than in the *Lobelia oligophylla* (11) and in the Mixed community 1 (12) (Figure 4a). The mean evenness was 0.5 (Figure 4b). It had one of the highest vegetation (95%, Figure 4c) and moisture indicators cover values (94%, Figure 4d).

2. *Rockhausenia pygmaea* community: A flat, firm cushion community formed by a dense aggregation of *Rockhausenia pygmaea* individuals, but not hummock forming. We did not observe pools close to it, but the soil surface was usually wet to the touch (soil moisture above 60%), and the third shallowest mean water table depth was recorded here. It was the second most common plant community. The mean richness per square meter was 8 (Figure 4a), and the evenness 0.70 (Figure 4b). Vegetation cover was 93%, while moisture indicators cover was 92% (Figure 4c, d). *Plantago tubulosa* and *Eleocharis albibracteata* were frequent companion species.
3. *Plantago rigida* community: A hard cushion community formed by densely aggregated *P. rigida* individuals devoid of pools. The surface was usually dry. The mean water table depth was close to the one in the *Aciachne* community, but *P. rigida* had the deepest record (-200 cm) in this study. The mean richness per plot (4) was the lowest among the thirteen communities. It was not significantly different only from the *Calamagrostis rigescens* (6) and *Calamagrostis chrysantha* (6) communities (Figure 4a). The mean evenness value of 0.38 was also the lowest among all communities (Figure 4b). Vegetation (92%) and moisture indicators (91%) cover were still high (Figure 4c, d).
4. *Plantago tubulosa* community: This flat, hard cushion community without pools has a usually wet surface with the highest record of soil moisture. Its mean richness per plot (8) and evenness values (0.69) were similar to those in most other communities (Figure 4a, b). Vegetation (92%, Figure 4c) and moisture indicators cover (89%, Figure 4d) were high.
5. *Lachemilla diplophylla* community: An herbaceous community, usually in sites with a water layer above the soil or with a very wet soil surface. The soil moisture was higher than in the *R. pygmaea* and *P. rigida* communities, but lower than in the *D. muscoides* community. The mean richness per plot was 7 (Figure 4a). Its evenness (0.61) was significantly lower than the one in Mixed community 1 (Figure 4b). The vegetation (94%, Figure 4c) and moisture indicators (93%, Figure 4d) cover were high.
6. *Aciachne pulvinata* community: A soft-cushion community. Cushions formed by *A. pulvinata* have usually a yellowish or light green color (the latter when plants are young), with sharp-pointed fruits that can produce pain (prick) when touched. The soil surface was always dry, without pools close to it. Nevertheless, soil moisture was close to those registered in some previous communities. The mean water table was the deepest recorded. The mean richness per plot was 8, while the evenness was 0.58 and only significantly lower than that of the two mixed communities. The vegetation and soil moisture indicators cover had lower values than most other communities, usually below 75% (Figure 4c, d).
7. *Juncus stipulatus* community: A rush (*Juncaceae*) community in permanently waterlogged areas (with water on the surface throughout the year). The soil

moisture was comparable with values observed in the *D. muscoides* community. The species richness per plot was relatively constant (Figure 4a), as well as the evenness which was high (0.75, Figure 4b). The vegetation and soil moisture indicators cover were high (91%, Figure 4c, d).

The following descriptions correspond to six potential communities we initially identified in our analyses (Group 2). To confirm the results, additional surveys and more plots from these communities will be required (currently, all have been recorded in one single plot, sampled annually).

8. *Calamagrostis rigescens* community: This community is dominated by a short tussock. The soil surface can be wet or dry. The mean richness per plot was one of the lowest (6), and the records were relatively constant in the surveyed period (Figure 4a), while the evenness was close to 0.5 (Figure 4b). Vegetation (98%) and moisture indicators (97%) cover were very high and constant (Figure 4c, d).
9. *Calamagrostis chrysantha* community: This community was dominated by a tall tussock, usually with a wet soil surface. The dominant species was commonly recorded growing in pools. The mean richness per plot was one of the lowest (6, Figure 4a). Vegetation and moisture indicators cover were high, and with low variability (89%, Figure 4c, d).
10. *Distichia filamentosa* community: This cushion community exhibits predominantly wet soil surfaces with pools close to it and was present in close proximity to a cryoturbated zone, i.e. subjected to a sequence of ice and thawing. It exhibited the highest soil moisture record together with *Plantago tubulosa* community. The mean richness per plot was 7 (Figure 4a), while the evenness was 0.76, one of the highest (Figure 4b). Vegetation, and moisture indicators cover indicators were very high (95%, Figure 4c, d).
11. *Lobelia oligophylla* community: This is an herbaceous community, usually with a wet surface. It had one of the highest records of mean richness per plot (11, Figure 4a) and evenness (0.78, Figure 4b). Vegetation (90%, Figure 4c) and moisture indicators (89%, Figure 4d) cover were high.
12. Mixed community 1: An herbaceous community with small tussocks of *Calamagrostis vicunarum*, some patches of herbaceous species (like *Lachemilla diplophylla*), and flat hard cushions of *Plantago tubulosa*. The soil surface was usually wet. Nevertheless, the soil moisture was the lowest recorded. The mean richness (12) and evenness (0.86) per plot were the highest recorded (Figure 4a, b). In this case, the cover of moisture indicators (72%) was much lower than the vegetation cover (89%), showing the presence of species that grow in drier areas.
13. Mixed community 2: An herbaceous community with sedges (*Eleocharis albibracteata*) and hard cushions of *Distichia muscoides*. The soil surface was usually wet, with a mean water table depth above -20 cm, but with its deepest record comparable to values found in the *R. pygmaea* community. The mean richness per plot was 8 (Figure 4a), and the evenness was high (0.71, Figure 4b), but not as much as in Mixed community 1. The vegetation (66%) and moisture indicators (65%) cover had the lowest records among all communities and were as variable as in the *Aciachne pulvinata* community (Figure 4c, d).

Patterns of diversity, structure, and composition of *bofedal* plant communities

We recorded 68 species belonging to 15 families and 45 genera (Suppl. material 3). The most species-rich family was *Poaceae* (24 species), followed by *Asteraceae* (10 species).

Group 1 communities' composition and dominance patterns remained stable and without significant statistical differences when assessed between years (Suppl. material 5, Figure 5, left panel). This pattern was also observed at the site (*bofedal*) level, where the identified communities showed an overall small contrast between years (Suppl. material 6). In contrast to the group 1 communities, group 2 displayed more variability in plant composition between the 2017 and the 2018–2019 surveys (Suppl. material 6).

The *Distichia muscoides* community was found in most of the sites (90%), plots (55%), and almost along the entire elevational range of our study (4,292–4,850 m a.s.l.). Other common plant communities were dominated by *Rockhausenia pygmaea* (42% of the sites, 18% plots), *Plantago rigida* (26% of the sites, 8% plots) and *Plantago tubulosa* (23% of the sites, 7% plots). The other nine plant communities were found in fewer than 17% of the sites and 12% of the plots (Table 2).

The communities with the highest mean richness were Mixed community 1 (12) and *Lobelia oligophylla* community (11), while *Plantago rigida* community (4) had the lowest values. Most communities had similar mean richness (7–8, Table 3), usually with no significant differences (Figure 4a). The species richness per plot ranged from 1 to 15. Nevertheless, 75% of the 1 m^2 plots had only 1–8 species; this included 79% of the *D. muscoides* community' plots and 100% of the *P. rigida*, *J. stipulatus* and *C. rigescens* communities' plots. Rarefaction curves showed consistent patterns; the *Plantago rigida* community displayed lower species richness compared to others. In contrast, these other communities exhibited similar species richness at lower sample sizes (Suppl. material 7). We highlight that communities shared most of their species (85–100%, Suppl. material 3). The Pielou index attained values between 0.38 (in *P. rigida* community) and 0.78 (*L. oligophylla* community, Table 3).

The species present in most *bofedales* (30 of 31 sites) were *D. muscoides*, *P. tubulosa* and *R. pygmaea*. Four species were most frequent per plot during our three-year

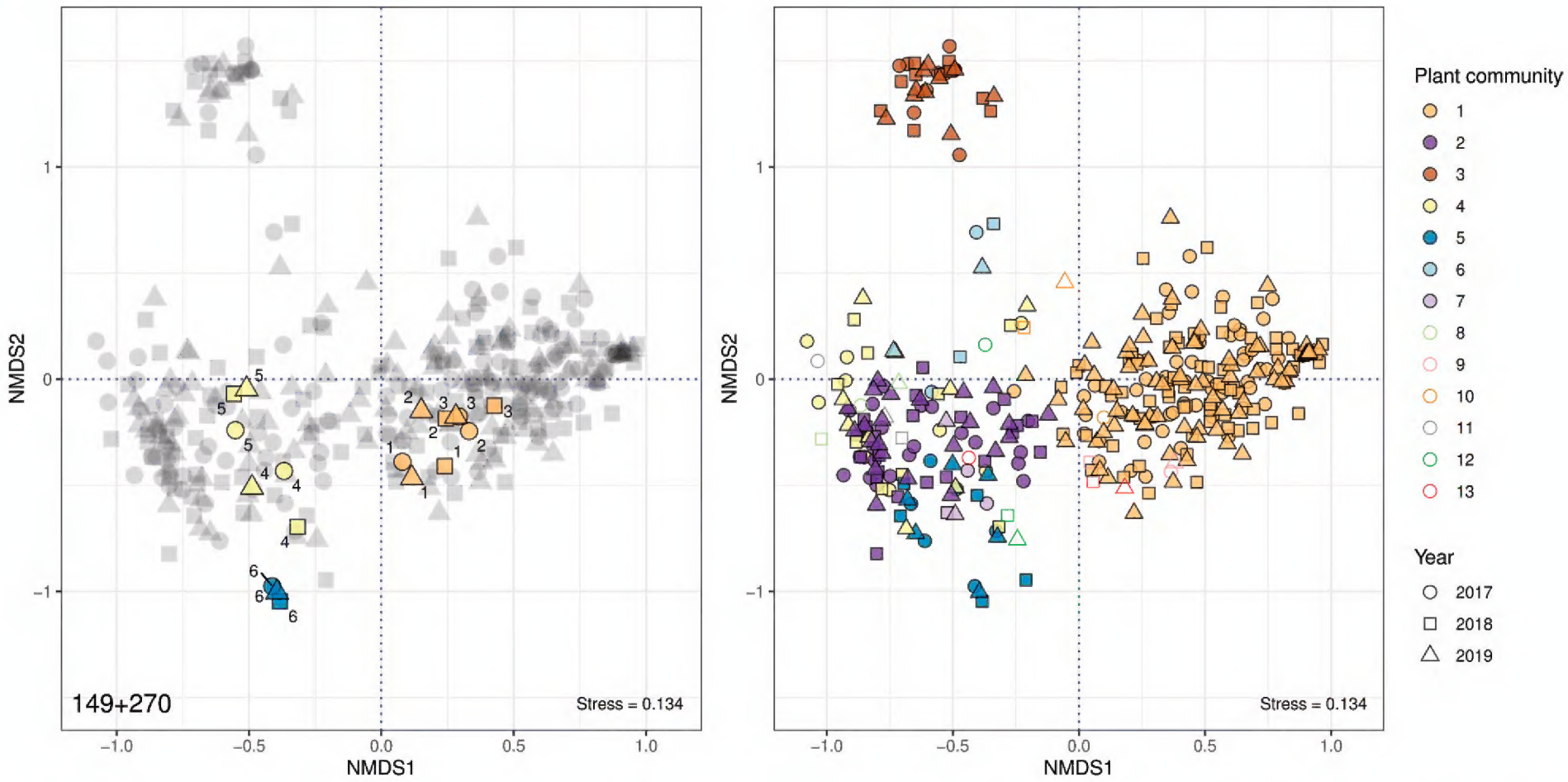

Figure 5. Species composition variability of the thirteen plant communities identified. NMDS based on Hellinger-transformed vegetation cover dissimilarities (Bray-Curtis distance) between 2017–2019. Left panel: Example of variation in plant composition of three plant communities present at 149+270 *bofedal*. Number indicates the same sampling location. Right panel: Variability of species composition across years. Filled symbols represent plant communities significantly different from each other. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2.

study: *Distichia muscoides* (occurred in 74% of all plots), *Plantago tubulosa* (69%), *Rockhausenia pygmaea* (63%) and *Lachemilla diplophylla* (51%). They were common companion species in most plant communities when they were not dominant (Table 4, Suppl. material 3).

Average plant cover was high in most plant communities (89–98%). The lowest values were recorded in the *Aciachne pulvinata* community (75%) and the Mixed community 2 (66%). The former had the highest values of dead cushions (11%), and the latter had the highest values of bare soil surfaces (33%, Table 2). These two cover types (dead cushions and bare soil) had cover values below 6% in all other plant communities. Other types of ground cover (water, mosses, dead plants, rock fragments, dung) had values below 9% and were thus considered less important in the study area.

Considering the data per year (Suppl. material 8), the variability of *bofedales* communities (PCA component 1) is defined by the cover of moisture indicator species (IH%, eigenvalue +0.54), overall plant cover (eigenvalue +0.52), and percentage of bare soil (eigenvalue -0.49). This first component clearly separates *Aciachne*, *Lobelia*, and mixed communities 1 and 2 from all other communities. The second component is defined by the species richness per plot (S, +0.68) and Pielou's evenness (J', +0.58), grouping the *P. rigida*, *C. chrysantha*, *C. rigescens*, *D. muscoides*, *Lachemilla diplophylla* and *A. pulvinata* communities.

Plant composition and abundance across *bofedales* and years showed a major dispersion in variability for *D. muscoides*, *R. pygmaea* and *P. tubulosa* communities, with a distinctive and less variable floristic assemblage for the *P. rigida* community (Figure 5, right panel). However, interannual variability is less evident within the same *bofedal*, for almost all identified communities (Figure 5, left panel, Suppl. material 6).

Soil moisture mean values per community were usually above 55%. The lowest values were recorded in the Mixed community 1 (20%) and in *Calamagrostis chrysantha* (45%); while *Plantago tubulosa* and *Distichia filamentosa* communities exhibited the highest values (100%). A Kruskal–Wallis test revealed only significant differences between the driest (Mixed community 1) and those over 60% of soil moisture (*Distichia muscoides*, *Rockhausenia pygmaea*, *Plantago tubulosa*, *Lachemilla diplophylla*, *Juncus stipulatus* and *Distichia filamentosa*). All other communities had overlapping values (Figure 6).

The months with the deepest water table record were September (-59±5 cm) and October (-55±9 cm). While the months with the shallowest water table were February (-5±1 cm) and December (-12±5 cm). The water table was deeper than 90 cm in the dry season, in at least one year in four of the five communities, with the only exception of *D. muscoides* community (Table 2). Mixed community 2 and *D. muscoides* had the shallowest mean water table depth (-19 cm). *P. rigida* (-43 cm) and *A. pulvinata* (-47 cm) communities had the deepest water table level. The water table reached depths greater than 130 cm in the dry season (Figure 6).

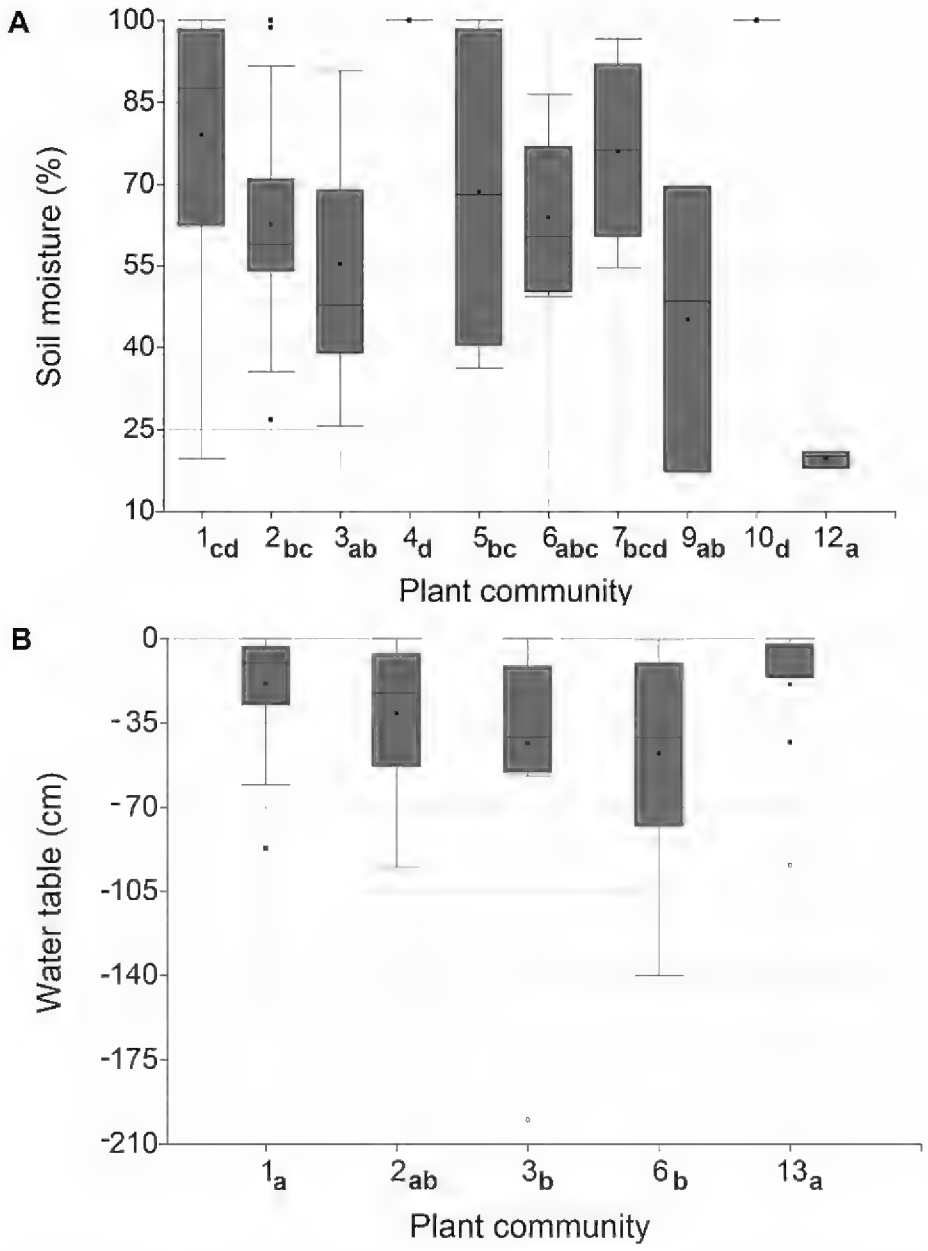

Figure 6. A) Soil moisture and B) water table depth per plant community. Plant communities: 1: *Distichia muscoides*, 2: *Rockhausenia pygmaea*, 3: *Plantago rigida*, 4: *Plantago tubulosa*, 5: *Lachemilla diplophylla*, 6: *Aciachne pulvinata*, 7: *Juncus stipulatus*, 8: *Calamagrostis rigescens*, 9: *Calamagrostis chrysantha*, 10: *Distichia filamentosa*, 11: *Lobelia oligophylla*, 12: Mixed community 1, 13: Mixed community 2. Communities with a common letter are not significantly different (Kruskal Wallis Test, $p > 0.05$). Inside each box, horizontal line and dot represent the median and mean values, respectively.

Discussion

The *bofedal* plant communities we characterize here along a southern Peruvian east–west Andean transect are heterogeneous as reported in studies across the Andes from Colombia (Cleef 1981; Benavides and Vitt 2014), Ecuador (Suarez et al. 2022), Peru (Cooper et al. 2010; Maldonado-Fonkén 2014; Salvador et al. 2014; Maldonado-Fonkén 2018; Polk et al. 2019; Portal-Quicaña 2019), Bolivia (Ruthsatz 2012; Loza Herrera et al. 2015; Domic et al. 2021), Chile (Squeo et al. 2006) and Argentina (Ruthsatz et al. 2020; Izquierdo et al. 2020; Izquierdo et al. 2022).

The seven plant communities (group 1) we identified (*Distichia muscoides*, *Rockhausenia pygmaea*, *Plantago rigida*, *Plantago tubulosa*, *Lachemilla diplophylla*, *Aciachne pulvinata* and *Juncus Stipulatus*) were consistent in their structural and compositional characteristics and maintained differences between them during our three-year study. The remaining six potential communities or group 2 (*Calamagrostis rigescens*, Mixed community 1, *Calamagrostis chrysantha*, *Distichia filamentosa*, *Lobelia oligophylla*, Mixed community 2) require additional surveys to resolve their status as independent communities. We include them here as some have been described previously with similar structural or compositional characteristics, such as communities of *Distichia filamentosa* in Bolivia (Ruthsatz 2012) or communities with either *Lobelia oligophylla* or *Calamagrostis tarmensis* in northern Peru as co-dominant species (Cooper et al. 2010).

All the dominant or co-dominant species of the thirteen plant communities we describe here, have been previously reported as key components in *bofedales* throughout South America, as will be discussed below, although not necessarily by being the most abundant or frequent species in the community.

The *Distichia muscoides* hard cushion community has been reported throughout Peru (INAIGEM 2023), including in areas close to our study sites (Maldonado-Fonkén 2014, 2018; Portal-Quicaña 2019). This community is found in South America following the wide geographical distribution of its distinctive species from Colombia to northern Argentina (Ruthsatz 2012). Nevertheless, it is not the only dominant species in *bofedales*, as shown in our study and other works in Colombia (Cleef 1981; Benavides and Vitt 2014), Ecuador (Suarez et al. 2022), Peru (Cooper et al. 2010; Maldonado-Fonkén 2014; Salvador et al. 2014; Polk et al. 2019; Portal-Quicaña 2019), Bolivia (Ruthsatz 2012; Loza Herrera et al. 2015), Chile (Squeo et al. 2006) and Argentina (Ruthsatz et al. 2020; Izquierdo et al. 2022). This community is present in sites rarely affected by saline stress (electrical conductivity 19–713 µS cm^{-1}), droughts, or frost (Salvador et al. 2014). The number of species previously reported per site in Bolivia and Peru was between 16–39 (Ruthsatz 2012), while we reported 3–28 species. The lowest species richness was found in sites with almost exclusive dominance of *D. muscoides*, with pools retaining considerable water even in the dry season and usually with soil moisture over 80%. Since *D. muscoides* is an aquatic plant (Leon and Young 1996), a shallow water table (and consequently, high soil moisture) could limit the development of other species with less tolerance for saturated conditions. High water tables favor peat accumulation enabling increased carbon capture and storage compared to sites with lower water tables. *D. muscoides* is dominant under very stable hydrological conditions and with a water level close to the surface, not deeper than 50 cm (Oyague 2021). Our study confirmed this, as this community had the shallowest mean water table, only three monitoring wells had values that exceeded 50 cm of depth in September 2017 or 2018.

Rockhausenia pygmaea is distributed from Venezuela to Argentina (Salvador et al. 2014) and is considered a characteristic species of *bofedales* (Ruthsatz 2012; Ruthsatz et al. 2020). It is a peat-forming species (Benavides and Vitt 2014) that grows forming carpets (Salvador et al. 2014), low-firm cushions to hummocks (Aubert et al. 2014). It was identified as a potential dominant species in the

Rockhausenia pygmaea–Pernettya prostrata assemblages in Ancash (Polk et al. 2019) and in the *Plantago tubulosa–Oreobolus obtusangulus–Rockhausenia pygmaea* assemblages in Cajamarca (Cooper et al. 2010), both in northern Peru. We recorded it as a dominant species and forming a recognizable community in 42% of the sites, being the second most common community after *Distichia muscoides*. Our records of soil moisture and water table suggest that it can thrive in drier conditions than *D. muscoides*.

Plantago rigida communities have been reported in Peru (Salvador et al. 2014), Ecuador (Suarez et al. 2022), and Colombia (Cleef 1981). According to Ruthsatz (2012), this species also grows at the edge of *bofedales* and in drier environments, and our results showed that it can thrive in drier conditions than *D. muscoides*. Nevertheless, Cleef (1981) reported it in wet depressions. In our study, it was the species with the highest abundance in its community and usually with fewer (less than five) companion species that can grow in the rare small openings between the leaves of this species or on the outside border of the cushions.

Plantago tubulosa is distributed along the Andes from Central America to Argentina (Cooper et al. 2010; Salvador et al. 2014) and is also considered a common species in *bofedales* (Ruthsatz et al. 2020). *P. tubulosa* communities have been reported from northern to southern Peru (Cooper et al. 2010; Salvador et al. 2014; Maldonado-Fonkén 2018), extending to Bolivia (Loza Herrera et al. 2015). However, it is most referred to as a co-dominant species in mixed communities with *Distichia muscoides* (Salvador et al. 2014) and *Oreobolus obtusangulus* (Polk et al. 2019), or in the *Plantago tubulosa–Oreobolus obtusangulus–Rockhausenia pygmaea* assemblage (Cooper et al. 2010). In our study, communities heavily dominated by *P. tubulosa* were found in 23% of the sites. This species also occurred as co-dominant with *Calamagrostis vicunarum* and *Lachemilla pinnata* in the Mixed community 1. Soil moisture was high and less variable than in the *D. muscoides* community; nevertheless, considering the lack of pools, we recommend additional studies about its water requirements.

Aciachne pulvinata was previously reported only as a companion species in *bofedales* in Peru (Cooper et al. 2010; Salvador et al. 2014) and Bolivia (Ruthsatz 2012). This species, associated with overgrazing (Salvador et al. 2014; Cochi Machaca et al. 2018), was present in eight of the 13 communities but was dominant only in one site with a low plant cover (75%) and the highest percentage of dead cushions (11%) recorded among the communities. Maldonado-Fonkén (2018) described a related community characterized by the sister taxon *Aciachne acicularis* in Ayacucho, where the percentage of litter and bare soil were at least 10% each, while the plant cover was 73%. We reported similar values in this study, despite the differences in survey methods. This community, together with *P. rigida*, had low water requirements. According to our observations, *A. pulvinata* increases its coverage in *bofedales* where the water level is decreasing.

Distichia filamentosa is distributed in Peru, Bolivia, and Chile (Ramirez 2011). This community has also been reported in those countries, growing at the upper growth limit of other cushion species (Squeo et al. 2006; Ruthsatz 2012; Loza Herrera et al. 2015). It has also been recorded in overgrazed areas in Bolivia (Cochi Machaca et al. 2018). We observed similar conditions in the only site where we identified this community: *D. filamentosa* was found at the extreme edge of the *bofedal*, next to a cryoturbated area, surrounded by *D. muscoides* cushions. Its water requirements seem to be high (soil moisture in dry season), but we recommend additional studies (water table measurements) in more sites. *Lobelia oligophylla* is distributed from Colombia to Bolivia and Chile (Cooper et al. 2010) and is considered a typical species of *bofedales* (Ruthsatz 2012). It was identified as a co-dominant species with the moss *Drepanocladus longifolius* in seasonally flooded areas in *bofedales* in Cajamarca (Cooper et al. 2010), and it is widely distributed in the peatlands of the Argentinean Puna (Izquierdo et al. 2020). In this study, we found it in a flat wet area but without any adjacent depressions or evidence of water courses that would indicate a potential to become a seasonally flooded area during the rainy season.

Juncus stipulatus, *Calamagrostis rigescens*, *Calamagrostis chrysantha* and *Lachemilla diplophylla* have been previously reported only as companion species in *bofedales* in Bolivia (Ruthsatz 2012) and Peru (Salvador et al. 2014). *C. rigescens* is also reported as a typical species of *bofedales* in Argentina (Ruthsatz et al. 2020) and is associated with overgrazing (Cochi Machaca et al. 2018). Species of the same genera, like *Juncus arcticus* or *Calamagrostis tarmensis*, have been previously described as co-dominant in *bofedales* communities in northern Peru (Cooper et al. 2010). In the case of rushes, they were found bordering lakes and ponds (Cooper et al. 2010). In our study, the *Juncus stipulatus* community was found in permanently waterlogged places but devoid of nearby pools. In contrast, the *Lachemilla diplophylla* community was usually found on wetter surfaces and moister areas, even recording the highest abundance of soil moisture indicators cover.

We encourage further study of the six preliminary communities (Group 2) to determine whether they result from local anthropogenic processes (e.g., overgrazing and draining) that increase the dominance of certain species or if more complex factors come into play (e.g., changes in water temperature and quality, regional climatic changes, etc.).

In most studies on *bofedales* vegetation, total species richness or mean richness per site is reported. These results are strongly influenced by the area assessed and sampling methods, which makes comparisons per area or sampling unit (e.g. square meter) difficult and shows an knowledge gap. Salvador et al. (2014) reported 56 species (vascular plants) in 24 sites, while Portal-Quicaña (2019) reported 85 species in one *bofedal* close to our study area. Our results (68 species in 27 sites) are similar to both studies. Other reports included 102 species in 36 sites (Cooper et al. 2010) and 119 species in 47 sites (Izquierdo et al. 2020). The number of species per 1 m^2 we found (1 to 15) is similar to what was reported in Argentina (1–13, Izquierdo et al. 2020). As reported in previous studies,

Poaceae and *Asteraceae* were the families with the most species (Maldonado-Fonkén 2018). Nevertheless, studies in Argentina, northern and central Peru included *Cyperaceae* as a third important family (Cooper et al. 2010; Polk et al. 2019; Izquierdo et al. 2020), which is much less conspicuously represented in our study.

Water table measurements per plant community in *bofedales* are uncommon, and this is the first report of soil moisture values. Although mentioned, details of the water table are usually not provided in published studies (e.g. Cooper et al. 2010). According to the recent classification proposed by INAIGEM (2023), the *bofedales* where we installed monitoring wells are considered seasonal because the water table is deeper than 20 cm for several months of the year. This suggests that water availability in our sites is strongly influenced by rainfall seasonality. This applies to 13 of 31 sites and five communities (*A. pulvinata*, *D. muscoides*, Mixed community 2, *P. rigida* and *R. pygmaea*). However, rainfall seasonality is probably not the only water source of these *bofedales*. Hillslope groundwater flowing from lateral moraines, talus, colluvium, or bedrock aquifers can also be a source (Cooper et al. 2019), especially because streams, lakes, and glaciers are uncommon in the area. Further hydrological studies are required to clarify the main water source of these *bofedales*.

Even though *bofedales* can be hydrologically seasonal, the dominant plants are perennial. Some have deep roots (e.g., *Distichia* spp., *Plantago* spp.) and can withstand periods without much water. In addition, the high content of organic matter or peat facilitates water storage. Therefore, the plant cover usually does not change over time significantly. Species richness could be more sensitive. If water is unavailable (too deep) for longer periods than the species can withstand, permanent changes can occur in the plant communities (e.g., dominant species, plant cover, etc.). A La Niña event (November 2017 to March 2018; IGP 2023), usually associated with droughts in southern Peru, provided an opportunity to test this. Our results showed this was not the case within our sites, with stable values over time. Furthermore, we learned that assessing the communities in the dry season (when resources are limited for plants), can give better information of their condition over time.

The concept of *bofedales* necessarily includes a set of several distinctive plant communities that respond to microenvironmental site characteristics (Cooper et al. 2010; Ruthsatz 2012; Salvador et al. 2014; Polk et al. 2019). We show that the heterogeneity in plant communities occurs at local site level, and also at landscape and regional scales, with 84% of our studied sites having 2–3 plant communities. Recognizing this vegetational heterogeneity is important for conservation, ecosystem management and/or restoration activities since it allows the establishment of reasonable goals according to the diversity, structural and compositional characteristics of the sites. Given the scarcity of regional-level surveys in Peru, our results constitute the first steps towards identifying useful indicators of vegetation characteristics for biological baseline development and monitoring. These indicators are essential for setting achievable and site-specific restoration goals and distinguishing relevant contributions of ecosystem services such as carbon storage, water regulation or grazing. To achieve this, we identified three key gaps in *bofedales* knowledge in Peru that need to be addressed in the short to medium term. First, we need to characterize the floristic variation across latitudinal and longitudinal gradients. We believe that there are several local studies describing the floristic composition of *bofedales* in several regions in Peru that make it possible to attempt an initial comprehensive analysis of plot-based studies at the national scale. Second, we need to improve the accuracy of remote-based sensor mapping of *bofedales*. Although the currently available official map of Peru's *bofedales* represents an important milestone, it inadequately describes the distribution and area of several bofedales in our study area. Some are misrepresented in terms of size or location, while others are not included at all. Third, the most complex challenge lies in understanding the various factors to which different *bofedales* plant communities respond, particularly those that define the structure and functioning of these unique ecosystems in a context of rapid land-use and climatic changes.

Data availability

Yearly plot-based species cover data have been deposited at Figshare and are publicly available (https://doi.org/10.25573/data.24512719). All other data used and mentioned in the manuscript are provided as Suppl. materials 1–8.

Author contributions

Conceptualization: M.M.F. and R.L.P.; methodology, formal analysis, writing-original draft preparation: M.M.F. and H.C.; data curation, field assessment: M.M.F.; writing-review and editing: M.M.F., R.L.P., H.C. and B.V. All authors have read and agreed to the published version of the manuscript.

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Supplementary material

Supplementary material 1
Examples of permanent plots (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl1

Supplementary material 2
Plot data (xlsx-file)
Link: https://doi.org/10.3897/VCS.115726.suppl2

Supplementary material 3
Information per plant community (xlsx-file)
Link: https://doi.org/10.3897/VCS.115726.suppl3

Supplementary material 4
Results (*p* and *R* values) of the One-way Analysis of Similarities (ANOSIM) between plant communities with Bray-Curtis index (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl4

Supplementary material 5
Results (*p* and *R*-values) of the One-way Analysis of Similarities (ANOSIM) between plant communities per year with Bray-Curtis index (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl5

Supplementary material 6
NMDS based on plant cover of the thirteen plant communities for each peatland evaluated between 2017–2019 (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl6

Supplementary material 7
Sample-based rarefaction curves (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl7

Supplementary material 8
Principal Component Analysis (pdf-file)
Link: https://doi.org/10.3897/VCS.115726.suppl8